Focus paper –2480 words excluding title, abstract and references

# Pollen taphonomy from hyaena scats and coprolites: preservation and quantitative differences.

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## Abstract

Coprolites are often used in African archaeological sites as archives for proxies like pollen, which are trapped and preserved inside them. Investigating pollen taphonomy, here we aim to aid interpretations of local and regional vegetation changes by assessing dietary and other pollen sources of fresh hyaena scats from the Tswalu Kalahari Reserve (TKR, South Africa) and coprolites from Equus Cave (South Africa). Our hypothesis is that the inner and outer fractions of coprolites possibly reflect qualitative and quantitative differences of dispersal factors of pollen taxa during the stages of scat formation influenced by hyaena behaviour and pollen sticking to wet surfaces after defecation. We mechanically separated the inner and outer sections of each scat and coprolite and extracted pollen from both fractions for analyses. The results were associated with vegetation maps of TKR and compared with pollen in modern soils, as controls, and quantitatively analysed in order to test potential differences in quality and richness of pollen between the inner and outer parts of samples. Scats and coprolites seem to be less biased sensors of vegetation than surface soil samples. Further, the inner parts of coprolites and scats provide significantly greater diversity of low pollen–producers including entomophilous types than the outer sections which may typically be biased by wind–transported types and less productive due to pollen loss by weathering. The core fraction might therefore be useful for representing the under–represented taxa in pollen assemblages from the surroundings where hyenas roam.

## Keywords

Palynology, Southern Africa, pollen-vegetation relationships, pollen dispersal, fossil dung, Kalahari.

# 1 Introduction

African environments are rich in archaeological finds but are unsuitable for fossil pollen preservation (Fleisher and Wynne-Jones, 2010) due to the absence of lake and wetland deposits, strong seasonal moisture variations and oxidation. Alternative archives are animal faeces, which can be preserved under dry conditions preventing microbial activity and oxidation of pollen walls (Linseele et al., 2013). Faeces of cows, hyraxes and hyaenas have been investigated in Southern Africa and contributed to a better understanding of Quaternary vegetation changes (e.g. Horowitz, 1992; Carrión et al., 2000; Gil-Romera et al., 2006, 2007; Scott & Woodborne, 2007; Quick et al., 2011; Chase et al., 2012).

Hyaena coprolites have been palynologically analysed in caves and better palynomorph preservation has been observed than in their surrounding mineral rich sediments (Scott, 1987; Scott and Brink, 1992; Carrión et al., 2000; Scott et al., 2003; Pesquero et al. 2011). Hyaena scats consist of an outer sticky tegumentary layer which hardens soon after exposure to the sun preserving the shape and seals the calcite and phosphate enriched bone-derived interior (Horwitz and Goldberg, 1989; Larkin et al., 2000; Pesquero et al., 2011; Mills and Hofer, 1992; Holekamp, K. pers. comm.). In open air hyaena coprolites are more solid and durable than herbivore coprolites where the elements weaken the outer layers (Harrison, 2011; Linseele et al., 2013). For accurate quantitative interpretations in environmental reconstructions, pollen trapping models in animal faeces may help to identify biases in pollen assemblages by dietary factors such as foraging areas, feeding habits, food availability and consequently corrosion caused by moisture fluctuations and oxidation. Different pollen inputs into the hyaena scats have been described briefly by Scott et al. (2003) e.g., a) dust on prey which enters the intestines, b) dust settling on scat after defecation, c) flowers in hyaena diet and d) incorporation of palynomorphs by drinking water (Fig. 1). Ingestion of pollen by devouring the rumen of prey is possible but less likely probably only occurring under extreme food shortage (Mills and Hofer, 1992; Skinner and Smithers, 1990; Holekamp, K., pers. comm.).

Pollen diversity in hyaena coprolites might reflect the regional vegetation better than herbivore coprolites which, depending on the species, tend to have restricted feeding habits (Scott, 1987; Dial et al., 1990; Hoeck and Parker, 1990; Kühn et al., 2013). Pollen inside the scats of omnivorous brown hyaenas derives from a wide area depending on their roaming and feeding behaviour. We expect that additional wind dispersed pollen from anemophilous taxa will stick on the surface of scats including that derived mostly from nearby and to a gradually declining degree from increasing distances away from the defecation site (Faegri and Iversen, 1989). The contribution of entomophilous plants, which produce less pollen, is thought to represent local vegetation to a smaller degree, e.g., via insects visiting the scats or lying on the skins.

In the case of fresh hyrax dung there seem to be differences in the inner and outer parts of dung pellets (Hubbard and Sampson, 1993), but in previous studies of hyaena coprolites, except in the case of the Malapa hominin site in the Sterkfontein Valley (Bamford et al., 2010), these fractions were not processed separately (González-Sampériz et al., 2003). The outer layer is usually removed to eliminate contamination loosing potential pollen rain information (Scott et al., 2003). Here our initial aim, as part of a wider on-going seasonal survey of pollen of recent hyena scats at Tswalu Kalahari Reserve (TKR) (Fig. 1), is to search for potential differences between the outer and inner layers for possible over-represented versus under-represented pollen inputs. We assume that the aerial pollen input might be significant and represents different wide surroundings where the animals roamed. This should show up on the scat surface while the pollen inside the scat will represent a mixture of plant taxa that could potentially be biased by diet e.g., ingested entomophilous types (Fig 1). In our study the available modern scats, however, may not represent a fully natural roaming range because the hyaenas consume carcases that were transported by rangers to one place. In order to obtain a more natural situation we include additional fossil brown hyena coprolites from Equus Cave, other than those previously studied by Scott (1987).

### *1.1. Hyaena ecology*

The feeding and social behaviour of hyenas are well studied (Kruuk, 1974; Mills, 2003; Wiesel, I, 2006; Holekamp, 2007; Kuhn, 2011). In Southern Africa, both spotted hyaena (*Crocuta crocuta*) and brown hyaena (*Hyaena brunnea)* occur. The former are restricted to sub-tropical semi-desert and woodland areas in Southern Africa and the latter are found in coastal, desert, semi-desert, scrub, open woodland and highveld areas. As predominantly solitary and nocturnal scavengers with an omnivorous diet that include insects, eggs, fruits, brown hyaenas roam up to 54.4 km away from their shelters hunting small sized mammals (from rodents to sub-adult springbok) and consuming pods and bark (Mills and Hofer, 1992).

# 2 Environmental settings

## 2.1 Geographical settings

### 2.1.2. The Tswalu Kalahari Reserve

Tswalu Kalahari Reserve (TKR) of c. 100 000 hectares (27° 13' 30' S and 22° 28' 40' E) lies in the Kalahari Desert, South Africa (Fig. 2a and b) with Proterozoic mountains and sandy plains of the Cenozoic Kalahari Group at an average altitude of 1200 m asl (van Rooyen et al. 2005). Samples were collected in the Gosberg Valley (Fig. 2). The climate is semi-arid with a mean annual precipitation and temperature of respectively 214 mm (mainly in summer) and ca. 19 °C (van Rooyen et al. 2005).

The studied valley has a hyaena den on its southern high-lying end. A feeding area where carcasses are dumped is situated ca. 200 m to the north (Fig 2b). According to local rangers, scats were produced by brown hyaenas. Spotted hyaenas are rare, being sighted intermittently or doubtfully (MacFadyen, pers.com).

The vegetation in the sampling area is Korana-Langberg Mountain Bushveld (Mucina and Rutherford 2006). Other units include Kathu Bushveld, Olifantshoek Plains Thornveld and Gordonia Duneveld (Fig 2). These units include *Acacia* trees (Mimosideae) and a variety of small shrubs and woody taxa like *Rhus* spp. -renamed *Searsia*- (Anacardiaceae), *Boscia albitrunca* (Capparaceae), *Terminalia sericea* (Capparaceae), *Acacia mellifera*, *A. karroo*, *A. erioloba* (Mimosoideae), *Grewia flava* (Tiliaceae), *Artemisia afra* (Asteraceae), and *Croton gratissimus* (Euphorbiaceae). Dominant grasses include *Eragrostis* spp. and *Arisitida* spp. (both Poaceae).

### 2.1.2 Equus Cave

The cave lies within the Savanna Biome in dolomites of the 100 m high Ghaap Escarpment at an altitude of 1250 masl (Figs 2a, b) in a tuffaceous deposit (Butzer, 1974). The semi-arid region has an annual precipitation of 425 mm. vegetation type at the cave is Ghaap Plateau Vaalbosveld (Mucina and Rutherford 2006), which includesCommon woody species likeof the Ghaap Plateau nearby the cave are *Acacia tortilis, A. mellifera* (Mimosoideae), *Tarchonanthus camphoratus* (Asteraceae), *Boscia albitrunca* (Capparaceae) and *Grewia flava* (Tiliaceae) (Fig 3).

# 3 Material and methods

## 3.1 Field methods

Eleven fresh hyaena scats were collected during September 2009. The collection transects a ca. 200 m distance towards the den. Three surface sediment samples were taken in this section to compare the general pollen rain with those of the scats. Seven Lateglacial and Holocene hyaena coprolites from Equus Cave (Fig 2a) were studied. Estimated coprolite ages in Table 1 are according to charcoal and ostrich eggshell dates compiled in Johnson et al. (1997) and age calibrations in Scott et al. (2012).

## 3.2 Laboratory methods

We separated the outer fractions of each scat and coprolite by cleaning with fine sand paper and collecting the dust, and using burins to extract a similar weight on the inside (ca. 5 g in each sample) (Fig 1 in annex A). The 39 samples [(11+7) x 2 plus 3 soil surface samples] were processed following a standard method including HF, KOH, HCl digestion and acetolysis. *Lycopodium* spore tablets were added to calculate the pollen concentration (Stockmarr, 1973). A mean of 280 pollen grains were counted (SD=76, maximum=381, minimum=204) under light microscope.

## 3.3 Numerical Analyses

### 3.3.1 Richness, concentration and differences between samples

Statistical analyses were performed with the packages Stats and Vegan from the software R v.2.5.0 (R Core Team, 2012). Pollen diversity was estimated through rarefaction analysis, which standardizes sample size and does not consider abundances of different pollen types (Birks and Line, 1992). We tested normality of the data with the Saphiro–Wilk test and then performed a one–way ANOVA (Table 1 in annex A) for analysis of variance between the pollen richness in the inner and outer parts (Jones and Bryant Jr, 2007).

### 3.3.2 Abundances of particular taxa between the two fractions of each hyaena sample

A paired t–test provided relevant differences on the abundance of the taxa between inner and outer samples focussing on those taxa that were > 0,5% in more than half of the samples and prominent in the current vegetation (see* in Fig 3). Detrended correspondence analysis (DCA) determined the length of the environmental gradient. As it was lower than 2.5 for each dataset analysed (Legendre and Gallagher, 2001), we assume that the taxa responses are linear. Principal components analysis (PCA) was performed on pollen counts from the inner and outer coprolites and soil samples using

IN, OUT and SURF respectively as explicative variables. Taxa used in the PCA were the same used for the t-test analyses.

# 4 Results and Discussion

Results obtained suggest that pollen preservation and concentration was better in scats and coprolites than in surface samples (average of $2.1\times10^{6}$ pollen grains/g versus $1.8\times10^{4}$ in surface samples). According to intuitive observations the outer sections of the samples appear to contain more eroded pollen grains than the inner fractions.

Figure 3 shows pollen percentages of the inner and outer fractions. The spectra obtained from the scats seem to represent the current vegetation of the area relatively well in terms of woody taxa (ranging between the 10–25 %), with a dominance of *Rhus* amongst the trees and Tubuliflora (Asteraceae) amongst small shrubs and herbs. The three surface samples have generally lower tree pollen percentages (ca. 10%) suggesting that entomophilous taxa (Table 2), are well represented in coprolites.

Visual inspection and ANOVA of the data does not suggest important dissimilarities in richness between the inner and outer sections (Table 1 in annex A). In contrast, the paired t-test performed for richness shows that particular taxa (Table 3) differed significantly between the two fractions, where the inner section presents, a larger number of species ($t=0.9166$, P-value=0.3772 with a $p>0.05$). This may seem counterintuitive as the external part of the scat is normally exposed to additional air-borne pollen or to pollen from insects visiting the scat. This could be due to quick drying of the sticky tegument and to pollen loss after exposure to the elements. We found significant differences in some selected taxa between the two sections (Table 3), e.g., amongst the trees, *Grewia* and *Rhus* and amongst the bushes, Liguliflora type (Asteraceae), Acanthaceae, Chenopodiaceae-Amaranthaceae type (Cheno/Ams). The PCA results are in agreement with these findings (Fig. 4) where Axis 1 and 2 explain ca. 89% and 6% respectively of the observed variance. The positive PCA values in Axis 1 show a higher number of less productive pollen taxa (Malvaceae, Portulacaceae, Asteraceae-liguliflorae, *Ruellia*-type) and relatively less arboreal elements. The latter (*Rhus*, Combretaceae, *Euclea*, *Commiphora* amongst others) and taxa with relatively higher pollen productivity (Poaceae) (Duffin and Bunting, 2008), are linked to negative values associated to the outer fractions and surface samples.

The mean abundance of the woody element *Grewia*, in the inner section, is one order of magnitude larger than in the outer fraction (Table 3), while the opposite applies for *Rhus*, where differences are significant (both p>0.01–Table 3, Fig. 4). This might reflect differences in vegetation between the roaming and defecation areas. It might also be related to differences in pollen productivity or differential preservation although both pollen types have strong exines. The family Anacardiaceae (including *Rhus* i.e. *Searsia*) is a relatively high pollen producer in the Kruger National Park (Duffin and Bunting, 2008).

Both Acanthaceae and Liguliflorae (Asteraceae) are more abundant in the outer than in the inner fractions with a lower level of significance (p>0.05, Table 3). In addition to differential pollen productivity and dispersal qualities, dietary habits of the hyaena's prey may account for the difference as both Acanthaceae and Asteraceae are not particularly edible for ruminants and other ungulates. In contrast Cheno/Am (Odhav et al., 2007) herbs, which have a significantly larger mean in the inner than in the outer sections (p>0.05), might be partly derived from the roaming area or dietary preference.

Charcoal particles (Fig. 3) are in some cases more abundant in the inner part of scats of coprolites possibly derived from areas that the hyaena's visited during roaming.

In general terms the inner section of the hyaena scats and coprolites seems to represent best the diversity of entomophilous taxa of the area as well as those with relatively lower pollen productivity (Table 2 and Fig 4). Despite lower richness, the outer sections reflect a higher abundance of trees and woody taxa, with relatively high pollen productivities and mixed pollinization strategies, as well as anemophilous species (Table 2).

We propose that when using coprolites in archaeological sites, saving the outer fractions might not be necessary unless the research question is to define representation of the abundance of local or regional plant types in the vegetation. The core of coprolites is likely to contain grains of low pollen producers and dispersers and the outer part more good pollen producers and long–distance dispersers. Future research should contribute to questions of the role of seasonality on the pollen inputs in coprolites as reported elsewhere by Velázquez and Bury (2012), and to the relationships of vegetation and pollen trapping in scats.

## 5 Conclusions

We tested quantitative and qualitative differences between pollen in the inner and outer sections in fresh scats and in Lateglacial–Early Holocene coprolites to assess their respective values as environmental proxies. We found the following:

- Confirmation that pollen preservation and amount was generally good both in fossil and fresh samples while surface samples presented smaller amounts of pollen.
- The inner section of the scats and coprolites showed a significantly larger number of taxa than the outer fraction and superficial samples. The inner fraction was better represented by entomophilous taxa or low pollen producers, which may reflect diverse dietary, behavioural, aerial and preservation factors. We confirm some variations between local and regional sources that may, therefore, be implied in our **findings even if contrasts between the hyena's scat and roaming areas at Tswalu is** not as big as found in pan or cave settings by Scott (1987) and by Scott and Brink, (1992)
- Separation of inner and outer fractions in hyaena coprolites might only be useful depending on the research focus.
- Ad–hoc methodological studies could aid palaeoenvironmental reconstructions.
- More taphonomic studies are needed to shed some light on the pollen–vegetation relationships of coprolites to refine data and interpretations.

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## Captions

Figure 1: Conceptual map of the different pollen inputs into the hyaena scat

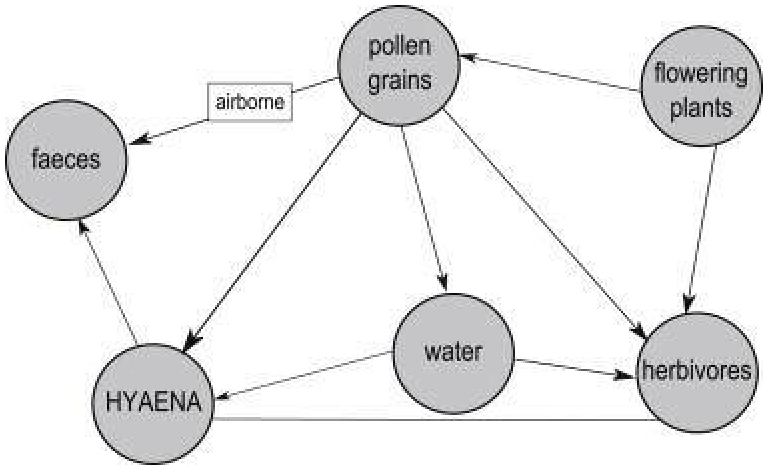


Figure 2: Localization of the two sites analysed in this study with the main vegetation biomes. and the Tswalu Kalahari Reserve where the transect for hyaena scat and surface sample collection is indicated.

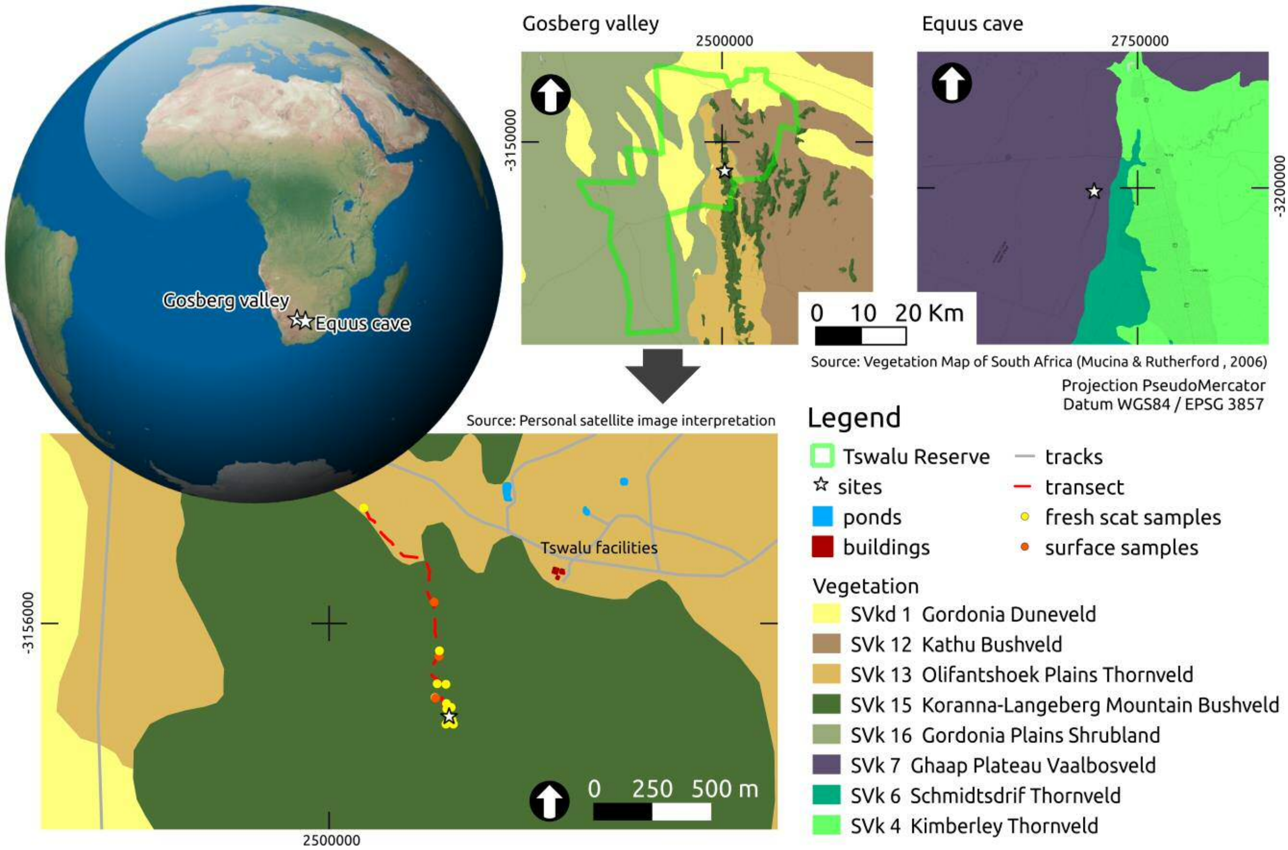

Figure 3: Percentage pollen diagram where the inner and outer section pollen assemblage is represented with different colours for every fresh scat (roman numbers) and fossil coprolites (notation EQ84–). The asterisk indicates taxa that were chosen for statisitical analyses.

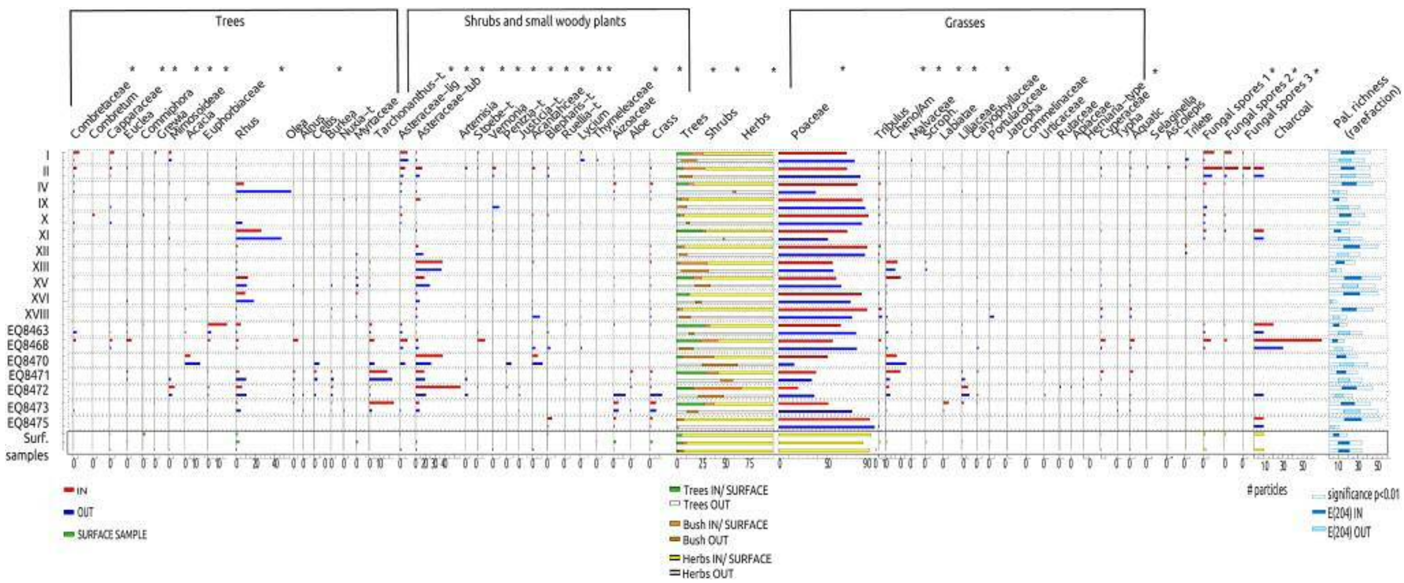


Figure 4: Biplot for the PCA where axis 1 and 2 explained 95% of the variance. Inner, outer or surface samples were used as explicative variables.

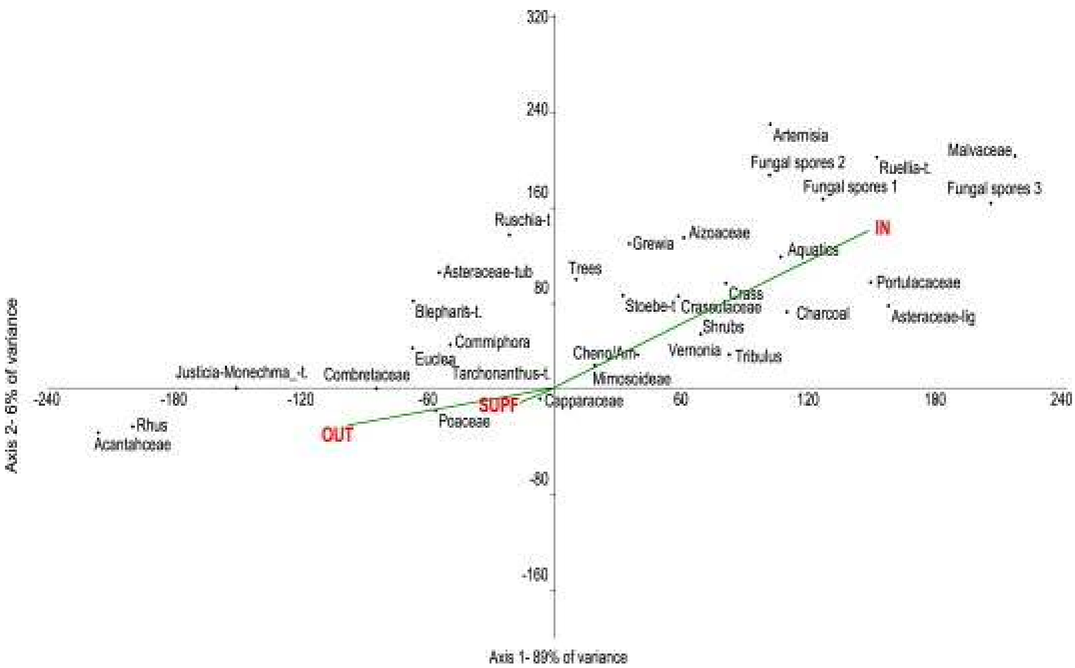

Table 1.

Age estimates of the coprolites found in Equus Cave based on radiocarbon dates (Scott, 1987 and Johnson et al., 1997) that were calibrated with CALP for the Southern Hemisphere (Talma and Vogel, 2006 and Scott et al., 2012).

| Sample code | Depth | Cal yr BP |
|---|---|---|
| EQ8463 | 67.5 | 11,090 |
| EQ8468 | 90 | 11,883 |
| EQ8470 | 97.5 | 13,049 |
| EQ8471 | 97.5 | 13,049 |
| EQ8472 | 105 | 14,169 |
| EQ8473 | 105 | 14,169 |
| EQ8475 | 112.5 | 15,288 |

Table 2.

Pollen dispersal strategies of the pollen types used in the PCA analysis. (This data were taken from Trigo et al., 2008,Velasco-Jiménez et al., 2013 and Watrin et al., 2007).

| Taxon | Pollen dispersal strategy | | | |
|---|---|---|---|---|
| | Anemophilous | Entomophilous | Mixed | Not known |
| Combretaceae | | | x | |
| Capparaceae | | | x | |
| Rhus | x | | | |
| Euclea | | | | x |
| Commiphora | x | | | |
| Grewia | | | x | |
| Mimosoideae | | x | | |
| Euphorbiaceae | | x | | |
| Olea | | | x | |
| Tarchonanthus-t | | | x | |
| Asteraceae (both types) | | x | | |
| Artemisia | | | x | |

| Taxon | Pollen dispersal strategy | | | |
|---|---|---|---|---|
| | Anemophilous | Entomophilous | Mixed | Not known |
| Stoebe-t | | x | | |
| Vernonia | | x | | |
| Pentzia-t. | | x | | |
| Acanthaceae (all taxa) | | x | | |
| Thymeleaceae | | x | | |
| Crassulaceae | | | x | |
| Poaceae | x | | | |
| Tribulus | | x | | |
| Chenopodiaceae/Amaranthaceae | | x | x | |
| Malvaceae | | x | | |
| Scrophulariaceae | | x | | |
| Liliaceae | | x | | |
| Cyperaceae | | | | x |

Table 3.

Results for the t-student analysis. Double asterisk indicates a significant result with a $p > 0.01$. Single asterisk indicates a significant result with a $p > 0.05$.

| | | Mean | $t$ | $p$–Value |
|---|---|---|---|---|
| Combretaceae | IN | 1.6667 | 0.2407 | 0.8127 |
| | OUT | 1.3889 | | |
| Capparaceae | IN | 1 | 0.06822 | 0.9464 |
| | OUT | 0.94444 | | |
| Grewia | IN | 0.5 | 1.512 | 0.1489** |
| | OUT | 0.055556 | | |
| Rhus | IN | 10.111 | −1.452 | 0.1646** |
| | OUT | 21.944 | | |
| Trees | IN | 28.667 | −0.4149 | 0.6834 |
| | OUT | 32.611 | | |
| Asteraceae–lig | IN | 2.6667 | −1.046 | 0.3101* |
| | OUT | 3.0556 | | |
| Asteraceae–tub | IN | 12.278 | 0.4135 | 0.6844 |
| | OUT | 10.833 | | |
| Acanthaceae | IN | 0.77778 | −0.9938 | 0.3343* |
| | OUT | 1.5 | | |
| Chamaephytes | IN | 18.222 | −0.3809 | 0.708 |

| | | Mean | *t* | *p*–Value |
|---|---|---|---|---|
| | OUT | 19.611 | | |
| Poaceae | IN | 131.44 | −0.7622 | 0.4564 |
| | OUT | 146.83 | | |
| Cheno–Am | IN | 5.3889 | 0.9012 | 0.3801* |
| | OUT | 3.5556 | | |
| Herbs | IN | 142.28 | 0.554 | 0.5868 |
| | OUT | 153.72 | | |
| Aquatics | IN | 1.1111 | 0.4826 | 0.6356 |
| | OUT | 0.94444 | | |
| Spores | IN | 9.3889 | 1.542 | 0.1416** |
| | OUT | 4.6111 | | |
| Charcoal | IN | 79.278 | −0.02665 | 0.979 |
| | OUT | 79.889 | | |
| Richness | IN | 13 | 0.9166 | 0.3722* |
| | OUT | 12.111 | | |
| | | | | |
| | | | | |

Figure 1 Annex: A: brown hyaena scats collected from Gosberg Valley. B: Extraction of the outer part of the scat (blue circle) using fine sandpaper. C: Extraction of the inner part of the scat (red arrow) using a metallic flat tip burin. D: Same process was followed with Equus cave coprolites. The extraction was made using gloves and masks, the table and metallic/ceramic tools used were cleaned with ethanol. All disposable material that could have been exposed to dust was thrown in a sealed plastic bag at each time before extraction of the inner part of the same scat/coprolite or before taking another specimen.


A
CM
B
C
D
S463

Table 1 anex. A: Results for the ANOVA analysis with all samples. The upper section indicates de 1–p value, while the bottom section indicates the F values.

| | I in | I out | II in | II out | IVa in | IVa out | IX in | IX out | X in | X out | XI in | XI out | XII in | XII out | XIII in | XIII out | XV in | XV out | XVI in | XVI out | XVIII in | XVIII out | EQ8463 in | EQ8463 out | EQ8468 in | EQ8468 out | EQ8470 in | EQ8470 out | EQ8471 in | EQ8471 out | EQ8472 in | EQ8472 out | EQ8473 in | EQ8473 out | EQ8475 in | EQ8475 out |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| I in | **0.000** | 1.000 | 1.000 | 1.000 | 1.000 | 1.000 | 1.000 | 1.000 | 1.000 | 1.000 | 1.000 | 1.000 | 1.000 | 1.000 | 1.000 | 1.000 | 1.000 | 1.000 | 1.000 | 1.000 | 1.000 | 1.000 | 1.000 | 1.000 | 1.000 | 1.000 | 1.000 | 1.000 | 1.000 | 1.000 | 1.000 | 1.000 | 1.000 | 1.000 | 1.000 | 1.000 |
| I out | 0.218 | **0.000** | 1.000 | 1.000 | 1.000 | 1.000 | 1.000 | 1.000 | 1.000 | 1.000 | 1.000 | 1.000 | 1.000 | 1.000 | 1.000 | 1.000 | 1.000 | 1.000 | 1.000 | 1.000 | 1.000 | 1.000 | 1.000 | 1.000 | 1.000 | 1.000 | 1.000 | 1.000 | 1.000 | 1.000 | 1.000 | 1.000 | 1.000 | 1.000 | 1.000 | 1.000 |
| II in | 0.241 | 0.460 | **0.000** | 1.000 | 1.000 | 1.000 | 1.000 | 1.000 | 1.000 | 1.000 | 1.000 | 1.000 | 1.000 | 1.000 | 1.000 | 1.000 | 1.000 | 1.000 | 1.000 | 1.000 | 1.000 | 1.000 | 1.000 | 1.000 | 1.000 | 1.000 | 1.000 | 1.000 | 1.000 | 1.000 | 1.000 | 1.000 | 1.000 | 1.000 | 1.000 | 1.000 |
| II out | 1.720 | 1.939 | 1.479 | **0.000** | 1.000 | 1.000 | 0.997 | 1.000 | 0.995 | 1.000 | 1.000 | 1.000 | 1.000 | 1.000 | 0.999 | 0.999 | 0.999 | 0.999 | 1.000 | 1.000 | 1.000 | 1.000 | 0.999 | 1.000 | 1.000 | 1.000 | 0.998 | 0.923 | 0.801 | 1.000 | 0.997 | 0.974 | 0.993 | 1.000 | 0.999 | 0.934 | 1.000 |
| IVa in | 0.157 | 0.375 | 0.085 | 1.564 | **0.000** | 1.000 | 1.000 | 1.000 | 1.000 | 1.000 | 1.000 | 1.000 | 1.000 | 1.000 | 1.000 | 1.000 | 1.000 | 1.000 | 1.000 | 1.000 | 1.000 | 1.000 | 1.000 | 1.000 | 1.000 | 1.000 | 1.000 | 1.000 | 1.000 | 1.000 | 1.000 | 1.000 | 1.000 | 1.000 | 1.000 | 1.000 |
| IVa out | 0.018 | 0.236 | 0.223 | 1.702 | 0.139 | **0.000** | 1.000 | 1.000 | 1.000 | 1.000 | 1.000 | 1.000 | 1.000 | 1.000 | 1.000 | 1.000 | 1.000 | 1.000 | 1.000 | 1.000 | 1.000 | 1.000 | 1.000 | 1.000 | 1.000 | 1.000 | 1.000 | 1.000 | 1.000 | 1.000 | 1.000 | 1.000 | 1.000 | 1.000 | 1.000 | 1.000 |
| IX in | 0.927 | 0.709 | 1.168 | 2.647 | 1.084 | 0.945 | **0.000** | 1.000 | 1.000 | 1.000 | 1.000 | 1.000 | 1.000 | 1.000 | 1.000 | 1.000 | 1.000 | 1.000 | 1.000 | 1.000 | 1.000 | 1.000 | 1.000 | 1.000 | 1.000 | 1.000 | 1.000 | 1.000 | 1.000 | 1.000 | 1.000 | 1.000 | 1.000 | 1.000 | 1.000 | 1.000 |
| IX out | 0.056 | 0.162 | 0.298 | 1.777 | 0.213 | 0.074 | 0.870 | **0.000** | 1.000 | 1.000 | 1.000 | 1.000 | 1.000 | 1.000 | 1.000 | 1.000 | 1.000 | 1.000 | 1.000 | 1.000 | 1.000 | 1.000 | 1.000 | 1.000 | 1.000 | 1.000 | 1.000 | 1.000 | 1.000 | 1.000 | 1.000 | 1.000 | 1.000 | 1.000 | 1.000 | 1.000 |
| X in | 1.027 | 0.809 | 1.268 | 2.747 | 1.184 | 1.045 | 0.100 | 0.971 | **0.000** | 1.000 | 1.000 | 1.000 | 1.000 | 1.000 | 1.000 | 1.000 | 1.000 | 1.000 | 1.000 | 1.000 | 1.000 | 1.000 | 1.000 | 1.000 | 1.000 | 1.000 | 1.000 | 1.000 | 1.000 | 1.000 | 1.000 | 1.000 | 1.000 | 1.000 | 1.000 | 1.000 |
| X out | 0.539 | 0.758 | 0.298 | 1.181 | 0.383 | 0.521 | 1.466 | 0.596 | 1.566 | **0.000** | 1.000 | 1.000 | 1.000 | 1.000 | 1.000 | 1.000 | 1.000 | 1.000 | 1.000 | 1.000 | 1.000 | 1.000 | 1.000 | 1.000 | 1.000 | 1.000 | 1.000 | 0.999 | 1.000 | 1.000 | 1.000 | 1.000 | 1.000 | 1.000 | 1.000 | 1.000 |
| XI in | 0.357 | 0.139 | 0.598 | 2.077 | 0.514 | 0.375 | 0.570 | 0.300 | 0.670 | 0.896 | **0.000** | 1.000 | 1.000 | 1.000 | 1.000 | 1.000 | 1.000 | 1.000 | 1.000 | 1.000 | 1.000 | 1.000 | 1.000 | 1.000 | 1.000 | 1.000 | 1.000 | 1.000 | 1.000 | 1.000 | 1.000 | 1.000 | 1.000 | 1.000 | 1.000 | 1.000 |
| XI out | 0.198 | 0.021 | 0.439 | 1.918 | 0.354 | 0.216 | 0.729 | 0.141 | 0.829 | 0.737 | 0.159 | **0.000** | 1.000 | 1.000 | 1.000 | 1.000 | 1.000 | 1.000 | 1.000 | 1.000 | 1.000 | 1.000 | 1.000 | 1.000 | 1.000 | 1.000 | 1.000 | 1.000 | 1.000 | 1.000 | 1.000 | 1.000 | 1.000 | 1.000 | 1.000 | 1.000 |
| XII in | 0.465 | 0.247 | 0.706 | 2.185 | 0.621 | 0.483 | 0.462 | 0.408 | 0.562 | 1.004 | 0.108 | 0.267 | **0.000** | 1.000 | 1.000 | 1.000 | 1.000 | 1.000 | 1.000 | 1.000 | 1.000 | 1.000 | 1.000 | 1.000 | 1.000 | 1.000 | 1.000 | 1.000 | 1.000 | 1.000 | 1.000 | 1.000 | 1.000 | 1.000 | 1.000 | 1.000 |
| XII out | 0.701 | 0.483 | 0.942 | 2.421 | 0.858 | 0.719 | 0.226 | 0.645 | 0.326 | 1.240 | 0.344 | 0.503 | 0.236 | **0.000** | 1.000 | 1.000 | 1.000 | 1.000 | 1.000 | 1.000 | 1.000 | 1.000 | 1.000 | 1.000 | 1.000 | 1.000 | 1.000 | 1.000 | 1.000 | 1.000 | 1.000 | 1.000 | 1.000 | 1.000 | 1.000 | 1.000 |
| XIII in | 0.840 | 0.621 | 1.081 | 2.560 | 0.996 | 0.858 | 0.087 | 0.783 | 0.187 | 1.379 | 0.483 | 0.642 | 0.375 | 0.139 | **0.000** | 1.000 | 1.000 | 1.000 | 1.000 | 1.000 | 1.000 | 1.000 | 1.000 | 1.000 | 1.000 | 1.000 | 1.000 | 1.000 | 1.000 | 1.000 | 1.000 | 1.000 | 1.000 | 1.000 | 1.000 | 1.000 |
| XIII out | 0.752 | 0.534 | 0.994 | 2.473 | 0.909 | 0.770 | 0.175 | 0.696 | 0.275 | 1.292 | 0.395 | 0.555 | 0.288 | 0.051 | 0.087 | **0.000** | 1.000 | 1.000 | 1.000 | 1.000 | 1.000 | 1.000 | 1.000 | 1.000 | 1.000 | 1.000 | 1.000 | 1.000 | 1.000 | 1.000 | 1.000 | 1.000 | 1.000 | 1.000 | 1.000 | 1.000 |
| XV in | 0.804 | 0.585 | 1.045 | 2.524 | 0.960 | 0.822 | 0.123 | 0.747 | 0.223 | 1.343 | 0.447 | 0.606 | 0.339 | 0.103 | 0.036 | 0.051 | **0.000** | 1.000 | 1.000 | 1.000 | 1.000 | 1.000 | 1.000 | 1.000 | 1.000 | 1.000 | 1.000 | 1.000 | 1.000 | 1.000 | 1.000 | 1.000 | 1.000 | 1.000 | 1.000 | 1.000 |
| XV out | 0.711 | 0.493 | 0.953 | 2.432 | 0.868 | 0.729 | 0.216 | 0.655 | 0.316 | 1.250 | 0.354 | 0.514 | 0.247 | 0.010 | 0.128 | 0.041 | 0.092 | **0.000** | 1.000 | 1.000 | 1.000 | 1.000 | 1.000 | 1.000 | 1.000 | 1.000 | 1.000 | 1.000 | 1.000 | 1.000 | 1.000 | 1.000 | 1.000 | 1.000 | 1.000 | 1.000 |
| XVI in | 1.081 | 1.299 | 0.840 | 0.639 | 0.924 | 1.063 | 2.008 | 1.137 | 2.108 | 0.542 | 1.438 | 1.279 | 1.546 | 1.782 | 1.921 | 1.833 | 1.885 | 1.792 | **0.000** | 1.000 | 1.000 | 1.000 | 1.000 | 1.000 | 1.000 | 1.000 | 0.997 | 0.978 | 1.000 | 1.000 | 1.000 | 1.000 | 1.000 | 1.000 | 0.997 | 1.000 |
| XVI out | 0.449 | 0.668 | 0.208 | 1.271 | 0.293 | 0.431 | 1.376 | 0.506 | 1.476 | 0.090 | 0.806 | 0.647 | 0.914 | 1.150 | 1.289 | 1.202 | 1.253 | 1.161 | 0.632 | **0.000** | 1.000 | 1.000 | 1.000 | 1.000 | 1.000 | 1.000 | 1.000 | 1.000 | 1.000 | 1.000 | 1.000 | 1.000 | 1.000 | 1.000 | 1.000 | 1.000 |
| XVIII in | 0.547 | 0.765 | 0.306 | 1.173 | 0.390 | 0.529 | 1.474 | 0.603 | 1.574 | 0.008 | 0.904 | 0.745 | 1.012 | 1.248 | 1.387 | 1.299 | 1.351 | 1.258 | 0.534 | 0.098 | **0.000** | 1.000 | 1.000 | 1.000 | 1.000 | 1.000 | 1.000 | 0.999 | 1.000 | 1.000 | 1.000 | 1.000 | 1.000 | 1.000 | 1.000 | 1.000 |
| XVIII out | 0.758 | 0.539 | 0.999 | 2.478 | 0.914 | 0.775 | 0.170 | 0.701 | 0.270 | 1.297 | 0.401 | 0.560 | 0.293 | 0.056 | 0.082 | 0.005 | 0.046 | 0.046 | 1.838 | 1.207 | 1.304 | **0.000** | 1.000 | 1.000 | 1.000 | 1.000 | 1.000 | 1.000 | 1.000 | 1.000 | 1.000 | 1.000 | 1.000 | 1.000 | 1.000 | 1.000 |
| EQ8463 in | 1.204 | 1.422 | 0.963 | 0.516 | 1.048 | 1.186 | 2.131 | 1.261 | 2.231 | 0.665 | 1.561 | 1.402 | 1.669 | 1.905 | 2.044 | 1.957 | 2.008 | 1.915 | 0.123 | 0.755 | 0.657 | 1.962 | **0.000** | 1.000 | 1.000 | 1.000 | 0.993 | 0.962 | 1.000 | 1.000 | 0.999 | 1.000 | 1.000 | 1.000 | 0.994 | 1.000 |
| EQ8463 out | 0.765 | 0.983 | 0.524 | 0.955 | 0.609 | 0.747 | 1.692 | 0.822 | 1.792 | 0.226 | 1.122 | 0.963 | 1.230 | 1.466 | 1.605 | 1.517 | 1.569 | 1.476 | 0.316 | 0.316 | 0.218 | 1.523 | 0.439 | **0.000** | 1.000 | 1.000 | 1.000 | 0.996 | 1.000 | 1.000 | 1.000 | 1.000 | 1.000 | 1.000 | 1.000 | 1.000 |
| EQ8468 in | 0.467 | 0.249 | 0.709 | 2.188 | 0.624 | 0.485 | 0.460 | 0.411 | 0.560 | 1.007 | 0.110 | 0.270 | 0.003 | 0.234 | 0.372 | 0.285 | 0.336 | 0.244 | 1.548 | 0.917 | 1.014 | 0.290 | 1.672 | 1.232 | **0.000** | 1.000 | 1.000 | 1.000 | 1.000 | 1.000 | 1.000 | 1.000 | 1.000 | 1.000 | 1.000 | 1.000 |
| EQ8468 out | 0.858 | 0.639 | 1.099 | 2.578 | 1.014 | 0.876 | 0.069 | 0.801 | 0.170 | 1.397 | 0.501 | 0.660 | 0.393 | 0.157 | 0.018 | 0.105 | 0.054 | 0.146 | 1.939 | 1.307 | 1.405 | 0.100 | 2.062 | 1.623 | 0.390 | **0.000** | 1.000 | 1.000 | 1.000 | 1.000 | 1.000 | 1.000 | 1.000 | 1.000 | 1.000 | 1.000 |
| EQ8470 in | 1.607 | 1.389 | 1.849 | 3.328 | 1.764 | 1.625 | 0.680 | 1.551 | 0.580 | 2.147 | 1.250 | 1.410 | 1.143 | 0.906 | 0.768 | 0.855 | 0.804 | 0.896 | 2.688 | 2.057 | 2.154 | 0.850 | 2.812 | 2.373 | 1.140 | 0.750 | **0.000** | 1.000 | 1.000 | 1.000 | 1.000 | 1.000 | 1.000 | 1.000 | 1.000 | 1.000 |
| EQ8470 out | 1.936 | 1.718 | 2.177 | 3.656 | 2.093 | 1.954 | 1.009 | 1.880 | 0.909 | 2.475 | 1.579 | 1.738 | 1.471 | 1.235 | 1.096 | 1.184 | 1.132 | 1.225 | 3.017 | 2.385 | 2.483 | 1.179 | 3.140 | 2.701 | 1.469 | 1.078 | 0.329 | **0.000** | 0.997 | 1.000 | 1.000 | 1.000 | 1.000 | 1.000 | 1.000 | 1.000 |
| EQ8471 in | 0.727 | 0.945 | 0.485 | 0.994 | 0.570 | 0.709 | 1.654 | 0.783 | 1.754 | 0.187 | 1.084 | 0.924 | 1.191 | 1.428 | 1.566 | 1.479 | 1.530 | 1.438 | 0.354 | 0.277 | 0.180 | 1.484 | 0.478 | 0.039 | 1.194 | 1.584 | 2.334 | 2.663 | **0.000** | 1.000 | 1.000 | 1.000 | 1.000 | 1.000 | 1.000 | 1.000 |
| EQ8471 out | 0.968 | 0.750 | 1.209 | 2.688 | 1.125 | 0.986 | 0.041 | 0.912 | 0.059 | 1.507 | 0.611 | 0.770 | 0.503 | 0.267 | 0.128 | 0.216 | 0.164 | 0.257 | 2.049 | 1.417 | 1.515 | 0.211 | 2.172 | 1.733 | 0.501 | 0.110 | 0.639 | 0.968 | 1.695 | **0.000** | 1.000 | 1.000 | 1.000 | 1.000 | 1.000 | 1.000 |
| EQ8472 in | 1.333 | 1.114 | 1.574 | 3.053 | 1.489 | 1.351 | 0.406 | 1.276 | 0.306 | 1.872 | 0.976 | 1.135 | 0.868 | 0.632 | 0.493 | 0.580 | 0.529 | 0.621 | 2.414 | 1.782 | 1.880 | 0.575 | 2.537 | 2.098 | 0.865 | 0.475 | 0.275 | 0.603 | 2.059 | 0.365 | **0.000** | 1.000 | 1.000 | 1.000 | 1.000 | 1.000 |
| EQ8472 out | 1.071 | 0.853 | 1.312 | 2.791 | 1.227 | 1.089 | 0.144 | 1.014 | 0.044 | 1.610 | 0.714 | 0.873 | 0.606 | 0.370 | 0.231 | 0.318 | 0.267 | 0.360 | 2.152 | 1.520 | 1.618 | 0.313 | 2.275 | 1.836 | 0.603 | 0.213 | 0.537 | 0.865 | 1.797 | 0.103 | 0.262 | **0.000** | 1.000 | 1.000 | 1.000 | 1.000 |
| EQ8473 in | 0.624 | 0.406 | 0.865 | 2.344 | 0.781 | 0.642 | 0.303 | 0.568 | 0.403 | 1.163 | 0.267 | 0.426 | 0.159 | 0.077 | 0.216 | 0.128 | 0.180 | 0.087 | 1.705 | 1.073 | 1.171 | 0.134 | 1.828 | 1.389 | 0.157 | 0.234 | 0.983 | 1.312 | 1.351 | 0.344 | 0.709 | 0.447 | **0.000** | 1.000 | 1.000 | 1.000 |
| EQ8473 out | 0.775 | 0.557 | 1.017 | 2.496 | 0.932 | 0.793 | 0.152 | 0.719 | 0.252 | 1.315 | 0.419 | 0.578 | 0.311 | 0.074 | 0.064 | 0.023 | 0.028 | 0.064 | 1.856 | 1.225 | 1.322 | 0.018 | 1.980 | 1.541 | 0.308 | 0.082 | 0.832 | 1.161 | 1.502 | 0.193 | 0.557 | 0.295 | 0.152 | **0.000** | 1.000 | 1.000 |
| EQ8475 in | 1.564 | 1.345 | 1.805 | 3.284 | 1.720 | 1.582 | 0.637 | 1.507 | 0.537 | 2.103 | 1.207 | 1.366 | 1.099 | 0.863 | 0.724 | 0.811 | 0.760 | 0.853 | 2.645 | 2.013 | 2.111 | 0.806 | 2.768 | 2.329 | 1.096 | 0.706 | 0.044 | 0.372 | 2.290 | 0.596 | 0.231 | 0.493 | 0.940 | 0.788 | **0.000** | 1.000 |
| EQ8475 out | 0.521 | 0.303 | 0.763 | 2.242 | 0.678 | 0.539 | 0.406 | 0.465 | 0.506 | 1.060 | 0.164 | 0.324 | 0.056 | 0.180 | 0.318 | 0.231 | 0.282 | 0.190 | 1.602 | 0.971 | 1.068 | 0.236 | 1.725 | 1.286 | 0.054 | 0.336 | 1.086 | 1.415 | 1.248 | 0.447 | 0.811 | 0.550 | 0.103 | 0.254 | 1.042 | **0.000** |